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ANALYSIS OF X- AND Y-LIKE VISUAL FUNCTION IN MAN USING THE CORT--ETC(U)
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FINAL TECHNICAL REPORT

Analysis of X- and Y-like Visual Function in Man using the Cortical Evoked Potential

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Abstract

A facility has been created which can objectively assess a human observer's acuity, contrast sensitivity, and neural transmission time between eye and brain, all by directly recording the brain's response with simple scalp electrodes. A start has been made in using these capabilities to separate responses originating in two subdivisions of the visual system, namely the divisions specialized for pattern and for movement perception. The techniques now have potential both for detecting disease and as a research tool for understanding visual function.

Introduction

Visual perception is the achievement of both eye and brain. It is in the eye's receptors that the all-important transduction from light to neural response occurs. The faint energy of an absorbed photon is amplified by little-understood biophysical processes to become a sweeping change in ion flow across the receptor membrane (see NAVAIR project, Lewis, 1980), while at the same time automatic gain controls keeps response levels from overloading the brain as we move from a darkened room to the beach at noon. The spatial array of ganglion cells' receptive fields in the retina sets the ultimate limit on visual acuity (see NAVAIR project, Wolbarsht & Ringo, 1979).

Ganglion cell output is relayed with relatively little change by the lateral geniculate nucleus (**LGN**) to the visual cortex. It is at the level of the cortex that cells can first be found which respond to such perceptually related cue detection tasks as the discrimination of contour orientation, depth in space, or motion across the visual field. The present project is concerned with the direct but non-invasive electrical recording of such cortical responses. The well-known visual evoked response (**VER,** also referred to as the **VEP,** visual evoked potential) is used to accomplish this recording, but the technique has been extended through changes in both the nature of the stimulation and the basis of the signal retrieval apparatus to obtain a far more detailed picture of visual performance than previously practical.

During the period of this contract, an existing VER facility was greatly changed and enhanced. We are now in the position to extract information from direct brain recording with a level of detail and precision previously attainable only with psychophysical techniques. While the sensitivity attainable with psychophysical testing remains superior to that attainable electrophysiologically, the techniques now developed have several advantages in the assessment of visual performance: 1) the test is objective and does not depend on the subject's report of what he can and cannot see; 2) the test is rapid; 3) because it is electrophysiological, the test has access to information about the substrate not available psychophysically, such as the conduction time of nerve pathways from eye to brain. Degradation of this conduction time is a valuable, early sign of diseases such as multiple sclerosis and tumors in the area of the optic chiasm.

After briefly introducing some aspects of basic visual science as they pertain to this project, the project's status in three chief areas is summarized. These areas are the measurement of acuity, the measurement of contrast threshold and MTF, and the measurement of apparent latency. ("MTF" refers to the modulation transfer function, which describes contrast threshold for various spatial frequencies, as explained below.)

Background

Evoked responses. As with hearing and somaesthesis (the body sense), we find in vision a large cortical area flooded with direct input from one receptor system only. In vision, the receptor system is comprised of the rods and cones of the retina. The input from the eyes to the so-called primary projection are in cortex is notable in several respects. A large area of tissue several centimeters across is innervated; the innervation arrives directly from the retina via a single synaptic relay; and the input is relatively uninfluenced by activity levels elsewhere in brain. This project capitalizes on several points which follow from these simple observations. First, because of the large amount of cortical tissue involved, one can in fact measure, at the scalp, potentials arising almost exclusively from visually stimulated brain activity. (Nevertheless, the retrieval of faint signals remains the chief technical problem in this project.) Second, from the directness and simplicity of pathways from eye to brain it follows that responses are well time-locked to stimuli. Knowing when to look for the faint response is the key to finding it. Our signal retrieval methods are based on this premise. As these direct responses are not filtered through large portions of the rest of the brain, the visually evoked responses, in particular the early-arriving components dealt with here, are relatively uninfluenced by the motivational state or attitude of the subject. Thus, provided the eyes remain fixated on and accommodated for the stimulus, the VER can be used to assess the basic sensitivities and capabilities of the visual apparatus. From this assessment, we can predict performance by a motivated observer in real-life situations.

Separate visual subsystems. Based on structure, physiological properties and probable visual function, cells in the retino-cortical projection may be divided into two groups, termed X and Y. Because of their very different roles in normal visual performance and possible differential involvement in disease, the initial application of the techniques developed in this project has been the dissociation of X- and Y-dominated evok?d responses. We wish to be able to measure these systems separately. This separation has been achieved for an acuity test and may also be seen in swept reversal rate data, as described below. However, many corroborative tests remain to be performed. Here, it is appropriate to present a simple caricature of the two systems.

The X system is well-adapted to support the highest acuity performance of the visual system, such as reading fine print. X cells were first defined at the retinal level as ganglion cells with linear summation of flux. Retinal ganglion cells have more or less circular receptive fields with two regions of opposite influence; if the central disk excites the neuron upon presentation of a particular stimulus, the annular region surrounding it will be inhibitory, and conversely. Although it is not logically required by the narrow linear flux summation definition, it follows in practice that the balance of center-surround response strength, the similarity in time of center-surround responses, and spatial linearity, all make these cells insensitive to low contrast targets (e.g., a real-life scene in smoke or fog). This is true even if the targets are moving. But if contrast is adequate, the relatively small absolute size of X-type ganglion cells' receptive fields endow them with high spatial resolution, a property further enhanced by the peaked sensitivity profiles typical of these cells.

X cells have properties as a class which suit them to high acuity tasks, quite apart from the refinement of the individual receptive fields. First, X cells are relatively numerous in the retina. Furthermore, like all classes of ganglion cells, X cells are more densely packed in the central retina (foveal area in monkey and man), but this foveation is probably more accentuated in X cells than in any other type. Apart from retinal factors, the importance of the X system for central vision is assured by their exclusive projection to cortical visual area 17 (striate cortex), whose vast neural machinery is more heavily weighted towards processing neural input from the foveal area then is any other area of the brain. In monkey and man, cortical areas concerned with color perception also receive X cell input almost exclusively.

The X pathways through the LGN to the cortex remain largely separate from Y pathways, and terminate in separate cortical layers. It is this separation right up the eye-to-brain pathway which justifies speaking not merely of this or that type of ganglion cell, but of separate <u>visual subsystems</u>. Ganglion cells with X-type electrophysiological properties are identified morphologically with smaller neurons termed beta cells. These cells with small somas and compact dendritic arborization give rise to finer diameter fibers, a difference which is maintained by relay cells in the LGN and <u>their</u> fibers in turn, so that the overall pathway is slower-conducting than the Y pathway. The ability to respond to rapidly moving or rapidly flashing stimuli is poorer in the X system.

The phasic response pattern and high conduction velocity of the Y system make this substrate well-adapted to mediate detection of rapid stimulus change, such as flicker and movement. The Y system also possess a projection to the superior colliculus, which itself is thought to play an important role in directing the eyes towards a target in peripheral vision (especially one which captures the attention by moving or flickering). The Y system is an al~~t~~erting system. A coarse, large target rapidly moving or flickering would be expected to differentially favor Y system response. Our apparatus is well-suited to varying flicker rates, coarseness of pattern and amount of contrast in order to favor one visual function over another.

Assessment of visual function

Origins of the technique. The conventional evoked response has been measured in the past with apparatus similar to that diagrammed in Fig. 1. Many light flashes from a strobe provoke many repeated electrical responses in the observer. Because of the stereotyped nature of the responses and their time-locked occurrence with respect to the time of the flash, the responses may be summed in a computer of average transients until they are large enough to be reliably measured against the obscuring background of the electroencephalogram (EEG) and other electrical noise.

The advantage of the simple flash-evoked visual potential is the potency of the stimulus: the sudden flash of light and return to darkness provokes a response which can be detected in spite of severe visual disability or technical inadequacy. Very different stimulation is required if one wishes to go beyond the assertion that the visual system is working to a quantitative assessment of pattern perception. Pattern reversal stimulation is an ideal choice. With this approach, a simple contour pattern, typically stripes on a checkerboard, is adjusted to have equal total amounts of black and white areas, and then made to undergo black-white reversal by any of several optical or electronic techniques. The lack of any change in overall brightness (the reversed image does not have more or brighter white areas than the original pattern) minimizes the contribution of the luminance-sensitive levels of the visual system. This accentuates the response from pattern-sensitive levels of the visual system neurons from which we may infer various pattern-related performance levels such as visual acuity.

Current approach. In concrete terms, our test situation is as follows. The subject views a black and white TV monitor which displays the output of a custom pattern generator. A typical pattern might be vertical stripes. The black and white stripes are complemented or reversed perhaps twelve times per second. This sudden pattern change, which does not involve any change in overall brightness, is a potent stimulus for the cortex. This is the response we retrieve from the background of the ongoing cerebral EEG, and other electrical noise in the body. Following the lead of Regan (1973, 1975) and Tyler et al. (1979), our advance in response recovery has been the abandonment of the more common computer averaging technique in favor of lock-in methods.

We use lock-in techniques to achieve rapid, almost real time retrieval of the VER. We have had to resolve several criticisms which are commonly leveled against this technique. The use of a quadrature lock-in with direct, separate computation of amplitude and phase avoids the objection--valid for simpler lock-in techniques--that phase shifts can be a spurious source of amplitude changes. The use of a highly linear multiplier based on pulse width modulation for the critical synchronous demodulation function of the lock-in makes it possible to achieve single-frequency response. This avoids the objection that the observed response amplitude is a mixture of unknown proportion of various harmonics, each of which may reflect independent, underlying generators. The single response frequency we most commonly select to study is the actual stimulus reversal rate.

The benefit of the lock-in approach is faster response. Instrument response is rapid enough to give us a glimpse of the brain's response as it occurs. This frees us in turn to make rapid, systematic, electronically-programmed changes in the stimulus. Most typically, we have reduced the visibility of the stimulus in some way, driving the evoked response down into the noise. The extrapolated point at which the VER amplitude would have been precisely zero is used to specify the observer's threshold for that stimulus. In practice, an observer will report he can no longer see the target at about the point where brain response would be zero according to this extrapolation technique.

The present instrumentation is summarized in Fig. 2. For stimulation, the pattern generator is driven both to rapidly reverse the stimulus and to slowly change its contrast (or spatial frequency; i.e., fineness of stripes). At the response end, signal retrieval is accomplished by a lock-in amplifier, with an averager used only as a transient event recorder to capture, store and plot a single sweep.

<u>Project status: assessment of visual function</u>

<u>Acuity.</u> Visual acuity may be assessed in 20 secs by gradually increasing the finess of stripes and observing the point at which the observed response falls to zero. The VER-determined acuity is almost twofold worse than acuity determined psychophysically for the same observer, provided he is experienced and cooperative enough for psychophysical testing. Thus if the observer reports he can resolve a fine pattern with as many as 32 cycles (black-white pairs of stripes) per degree of subtended visual angle, the VER test will show a threshold of perhaps 16 cycles/degree (cpd). We have now established that this difference is consistent for weak and strong eyes of the same observer, for different observers, and for changes in refractive state. Thus, while it is less sensitive, the VER reliably measures changes in level of acuity and can predict psychophysical acuity

simply by multiplying measured thresholds by two.

An acuity determination is illustrated in Fig. 3. Linear decrease in VER amplitude unambiguously defines a zero-amplitude point at 15.2 sec. After 15.2 sec, spatial frequency has reached a finess of stripes equal to 25.3 cpd. Instrumental delay poses a technical problem: as the instrument takes approximately 6 secs to respond, zero amplitude was actually reached by the brain at an earlier time when spatial frequency was 17.6 cpd. This problem will be solved in future by sweeping the parameter under test both upwards (to finer stripes) and downwards, and then averaging the results. The artifactual shifts occur in opposite directions and will cancel. The cancellation of instrument delay in this manner waits upon more flexible computer of the laboratory.

Contrast threshold and the MTF. Contrast threshold for a given spatial pattern is assessed analogously to the acuity limit. During a 20 second period of data collection, the pattern's contrast is faded into invisibility. A contrast change which is a logarithmic function of time linearizes the VER response (Campbell & Maffei, 1970). Simple inspection can then specify the zero-amplitude point which defines visual threshold.

Contrast threshold determination is a significant advance over traditional acuity testing. An analogy with high fidelity amplifier evaluation makes this clearer. Once we know the quantity of the amplifier output (watts), how can its quality be measured? A first step would be the specification of the unit's high frequency response. This is analogous to specifying a human observer's acuity limit, as very fine details in very small targets are composed of high frequencies too, but in the visual realm, these are high spatial frequencies. For the amplifier, maximum frequency response tells us little of the unit's ability to provide a satisfactory rendition of speech or music--complex, everyday signals containing many frequencies. The amplifier's gain at all frequencies within its passband--not just the upper and lower limits themselves--provide the means to evaluate the amplifier's performance with any signal. The gain at all frequencies within an instrument's passband is termed its MTF (strictly, the MTF also includes a specification of phase shift at all frequencies). The shape of any signal after it has been passed through an amplifier may be quantitatively predicted from the amplifier's MTF. The analogous measure in vision is the contrast sensitivity function for all spatial frequencies. The contrast sensitivity function is obtained by determining the contrast threshold for a succession of sinusoidal (blurry-edged) striped patterns, ranging from very fine stripes close to the acuity limit to coarse stripes.

Two advantages of the visual MTF are 1) that response to any real-life stimulus may be predicted from the information it provides and 2) it is presently emerging that a variety of diseases, particularly in their earlier stages, may depress sensitivity at some spatial frequencies but not others. If it is only coarse stripes which come to require higher contrast before they can be detected by a given observer, the problem will never be detected by conventional acuity testing, yet the observer has a problem. Such an observer who is "low frequency anomalous," will not be able to detect large, "obvious" targets in smoke or fog . MTF testing thus has advantages in detecting visual disabilities which arise in certain visual and nervous system diseases. For this reason, it has received increasing attention clinically, both in civilian and aerospace medicine (Ginsburg, 1978).

In this project, we have now been able to measure the visual MTF with objective brain recordings. This entails making contrast threshold determinations at a succession of spatial frequencies. The contrast sensitivity function for one observer, shown in Fig. 4 is in good agreement with MTFs reported by other laboratories and obtained by conventional psychophysical methods. The sensitivity of the direct-recording technique is less by a factor of about 4 than the thresholds obtained by asking a trained observer to report what he sees, but the shape and behaviour of the function are correct , and the results are repeatable. This capability will be applied to both basic visual research and to clinical screening. Its potential to obtain a 6-point MTF in 3 minutes can not be realized, however, until the present facility is computer automated.

<u>Apparent latency.</u> The finite conduction time from eye to brain dictates that the electrical response observed at the subject's scalp is delayed--or shifted in phase--with respect to the visual stimulus. Knowing this delay is important in both basic visual science as an indication of which visual subsystem pathway (X or Y) is making the dominant contribution to the observed response, and in clinical assessment as an indication of disease and degeneration in and around neural pathways. Unfortunately, it is impossible to identify the amount of temporal shift between the visual input and the observed response by simple inspection. Consider the stimulus reversal signal and the train of oscillatory scalp potential responses. The two signal trains may be imperfectly aligned by, say, a quarter cycle (i.e., a 90 degree phase shift), but is this because the response has slipped behind by ten full cycles <u>plus</u> 90 deg or by just 90 deg?

The inference of retino-cortical latency from phase shift requires that the ambiguity identifying particular, corresponding elements in stimulus and response trains be surmounted. This may be done by changing the reversal rate itself. Suppose retino-cortical latency is so long with respect to reversal rate that ten reversals have occurred before the response to the initial reversal appears for observation at the scalp electrodes. Suppose the reversal rate is now slightly increased, so that the time period between reversals is shorter than before by some small fraction of a cycle--say 18 degs. If 10 cycles are in the pipeline from eye to brain, an 18 deg reduction in the period of each cycle will produce an observed phase shift overall of 180 deg. In practice, we now electronically sweep reversal rate over a 10 Hz range, and derive latency from the expression latency(secs)=(degs/360) x period,

where degs are the total number of degrees phase shift observed and period is the period of the frequency change (0.1 sec for 10 Hz), not the period of the actual reversal rate, which might have been swept from 2 to 12 Hz, or 15 to 25 Hz. (In this Report, "Hz" is used synonymously with "reversal rate." With this usage, the frequency of the steady-state response to a 15 Hz stimulus is the same as the frequency of the response to a 15 reversals/sec stimulus.) The results of such a determination are shown in Fig. 5. Earlier technical difficulties which caused enormous phase artifacts at sweep onset have been eliminated. This capability will now be used in both clinically applied and basic visual research. In particular, we will look for shifts to shorter latency under spatial conditions (coarse stripes, lower contrast) and temporal conditions (high reversal rate) which favor Y system response (cf. Shapley & Victor, 1978).

Project status: separation of X & Y function

The oblique effect is a subtle but all-pervasive phenomenon in visual contour perception (Appelle,1972). Performance on a wide variety of visual tasks is reduced when the dominant contours of the test stimulus are oblique rather than horizontal or vertical. For stripes, this means that acuity is poorer and contrast thresholds are higher for oblique stripes, based on older psychophysical testing methods. The elevation contrast threshold has also been shown electrophysiologically in man with the VER, using lengthy, repeated tests at a succession of fixed contrast levels (Maffei & Campbell, 1970). For acuity, our swept techniques are sensitive enough to show the oblique effect by simply taking a 20-second sweep at a horizontal or vertical orientation and then repeating the run after rotating the stimulus to an oblique orientation.

The oblique effect appears to be the result of some X-system property or properties, such as greater numbers of cortical cells with HV preference (Leventhal & Hirsch, 1977), or stronger intracortical interactions among these units, a pair of possibilities which may in fact be interrelated during cortical development (Nelson, 1978). The evidence for an X system origin of the oblique effect comes both from psychophysics and neurophysiology. Psychophysically, it has been shown that the oblique effect is strongest in central vision (Berkeley, Kitterle & Watkins, 1975), and at slow temporal modulation rates (Camisa, Blake & Lema, 1977), both conditions where in the X system plays a dominant role. Electrophysiologically, it has been shown in monkeys that simple cells in the central projection area have a strong horizontal/vertical bias (Mansfield, 1974; Mansfield & Ronner, 1978). This type of cell in this projection area is believed to be predominantly X-innervated. Thus the X system is probably making a strong contribution to the observed VER when the oblique effect is demonstrable, as in Fig. 6. We hypothesized that the same test repeated at a higher reversal rate would abolish the oblique effect. This hypothesis has now been confirmed. There is no reliable HV-vs.-oblique difference in VER-assessed acuity when acuity determinations are made at 42 rather than 7 reversals/sec (Fig. 7). This test needs to be confirmed in other observers, extended from acuity to contrast threshold behavior, and confirmed with other indications of XY differences. For example, the masking of the central region of the stimulus (i.e., a disk of cardboard centered on the fixation point) should more greatly attenuate response amplitude under conditions which elicit the oblique effect than otherwise, as the oblique effect indicates a large X contribution to the observed response, and the X system looks preferentially at a central stimuli.

Reversal rate. A simple reversal rate experiment also provides evidence for separate X Y response. We selected the two reversal rates above after first using our swept technique to examine response across a wide frequency range embracing almost all possible reversal rates. The response when a coarse spatial pattern was used is shown in Fig. 8. As temporal rate climbs out of EEG alpha bands, response amplitude falls. There is, however, a resurgence of response at very high reversal rates. Is this a Y system response at high temporal frequencies? This hypothesis is easily tested. If the response peak at 43 reversals/sec is caused by the Y system, the use of a pattern unfavorable to the Y system should abolish the peak. Fine stripes are an unfavorable Y system stimulus. Repeating the experiment of Fig. 8, but with a 10 cpd rather than a 1 cpd grating abolishes the 43 reversals/sec peak. The 43 reversals/sec peak behaves like a Y-dominated response. This is what convinced us to use 43 and 7 reversals/sec for the acuity tests. In effect, the oblique effect provides an independent means of labeling a particular peak as X or Y dominated. So we can now be confident that 7 Hz responses at the acuity limit are X dominated, and 43 Hz responses are not.

Summary

Techniques now developed have given us the power to sweep the entire spatio-temporal landscape of visual performance, measuring spatial contrast and temporal modulation thresholds at any point, that is, for any given spatial pattern and reversal rate. The work with the oblique and other effects provide an independent means of selecting precisely those combinations of parameters which most favor and best separate X-and Y-dominated responses. Routine application of these techniques in a way which takes advantage of their inherent speed must wait upon computer automation of the facility. Nevertheless, at a laboratory research level, a tool has been created for basic research, and for visual assessment of normal and clinical observers. Future applications include 1) screening for visual performance deficits in motion detection in real-life, low visibility conditions; 2) clinical screening and diagnosis; 3) study of the relationship of EEG activity to visually-evoked activity, of importance in the human centrifuge project at the Naval Air Development Center in Warminster, PA; and 4) separation of the involvement of X and Y visual subsystems in normal visual performance, and in neuro-ophthalmological disease.

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FIGURES

Fig. 1. Conventional Visual Evoked Response (**VER**) with strobe stimulation. Although a pattern or silhouette might be placed in front of the strobe lamp, the stimulation still involves abrupt luminance changes which are a potent stimulus to all levels of the visual system. A strong stimulus similar to this one is used in the NAVAIR human centrifuge project. On the other hand, pure pattern stimulation without average luminance change is more appropriate to assessing perceptual skills such as visual acuity.

Fig. 2. Instrumentation for the present project. A TV-type stimulator presents pattern stimulation with no net change in average luminance. Signal retrieval is performed by a lock-in amplifier rather than a computer of average transients.

Fig. 3. Assessment of visual acuity. VER amplitude decreases as fineness of stripes is steadily increased over a period of 20 seconds. At a spatial frequency of 25.3 cycles per degree (**cpd**) the amplitude has fallen to zero, indicating the acuity limit of this subject. Pattern reversal rate 12.7 Hz, 40% contrast.

Fig. 4. Modulation Transfer Function (**MTF**). The MTF measured with the swept contrast VER technique (circles, 18 Hz) has the same general shape as the MTF obtained with conventional subjective psychophysical techniques (diamonds, Koenderink & van Doorn, 1980, 7 Hz; circles, broken line, Sekuler & Tynan, 1977, 6 Hz). The VER technique is approximately 4 times less sensitive, but it is reliable, rapid and objective.

Fig. 5. Latency. Eye to brain latency may be measured from the phase shift observed as reversal rate is slightly increased. Sine grating 1 cpd, 80% contrast. An advantage of this technique is its immunity to waveform change, since a particular peak need not be identified as the arbitrary "beginning" of the response. Consequently, latency testing may now be carried out over an extremely wide range of stimulation conditions.

Fig. 6. The oblique effect. Acuity is poorer for oblique contours than for horizontal/vertical contours, and this small acuity difference may be detected with the scanned stimulus VER technique. The reversal rate for this test was set to the low value of 7 Hz. 80% contrast sine wave grating. Solid lines, horizontal/vertical gratings; broken lines, two runs of left oblique gratings. Reliable responses could not be obtained for right oblique gratings.

Fig. 7. No oblique effect could be obtained at a 42 Hz reversal rate. H, V, LO: extrapolated acuity limits for horizontal, vertical and left oblique sine gratings, 100% contrast. Acuity is not superior for horizontal/vertical. This indicates that the response being recorded under these conditions is not X-dominated, but instead probably comes from Y-type visual neurons with a relatively great weighting for peripheral vision. Again, reliable responses could not be obtained for right oblique gratings.

Fig. 8. Conspicuous response at the rapid reversal rate of 43 Hz (right side of Figure) in subject IS. A relatively coarse grating of 1 cpd (at 60% contrast) was used. With the oblique effect test of the previous two figures, we can now surmise that the second peak is the product of the second visual subsystem; i.e., Y-type neurons in peristriate cortex. We next hope to corroborate this hypothesis with tests of latency and peripheral/central visual field weighting.

Fig. 9. The response peak at 43 Hz disappears when spatial frequency is raised to 10 cpd. The inability of fine stripes to sustain the 43 Hz peak is further evidence that it arises from the poor-resolution Y system. Contrast 60%.

FIG 1

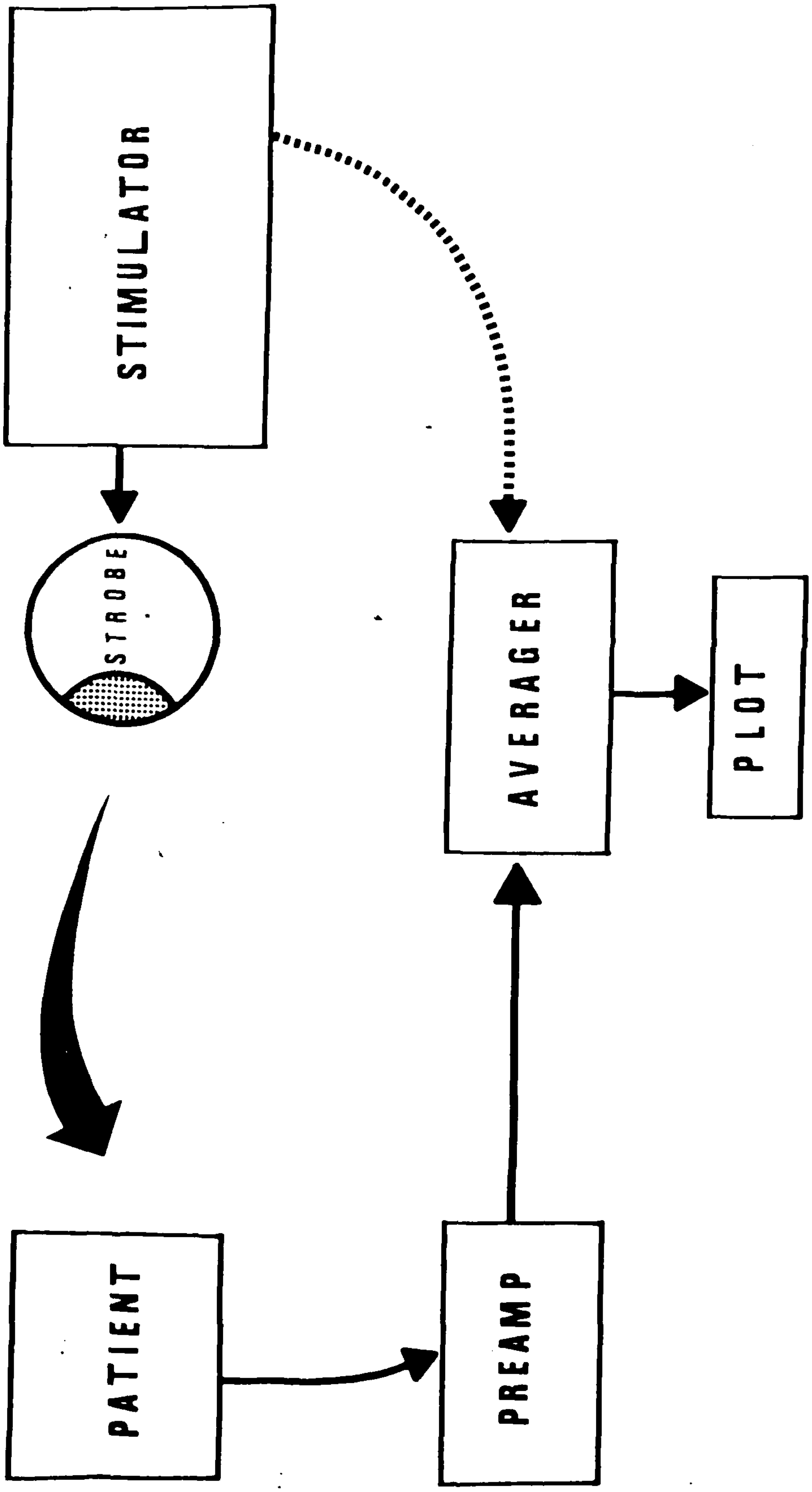

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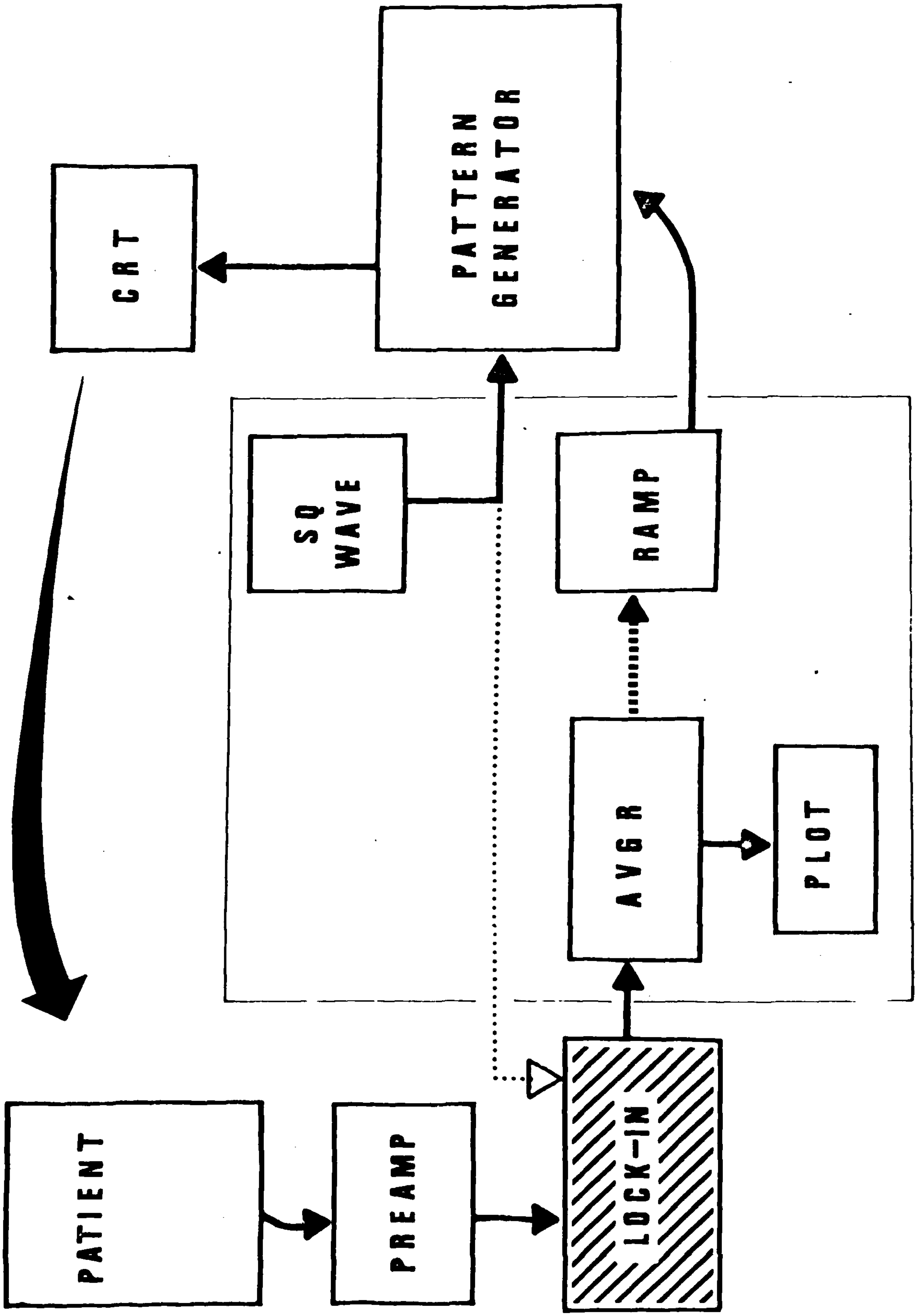
FIG. 2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PATTERN GENERATOR
SQ WAVE
RAMP
AVGR
PLOT
PATIENT
PREAMP
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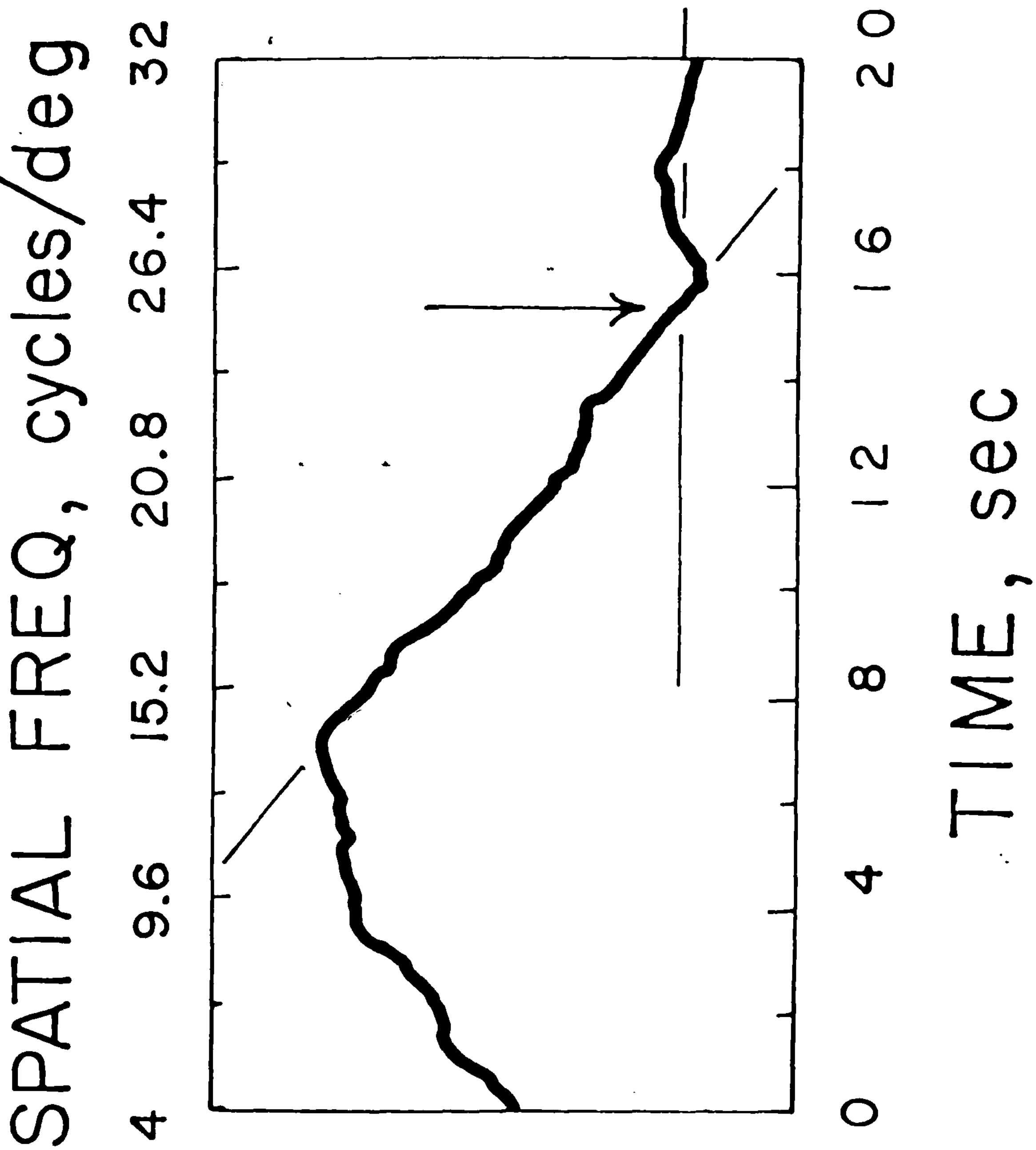
SPATIAL FREQ, cycles/deg
4 9.6 15.2 20.8 26.4 32
TIME, sec
0 4 8 12 16 20

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Fig. 4

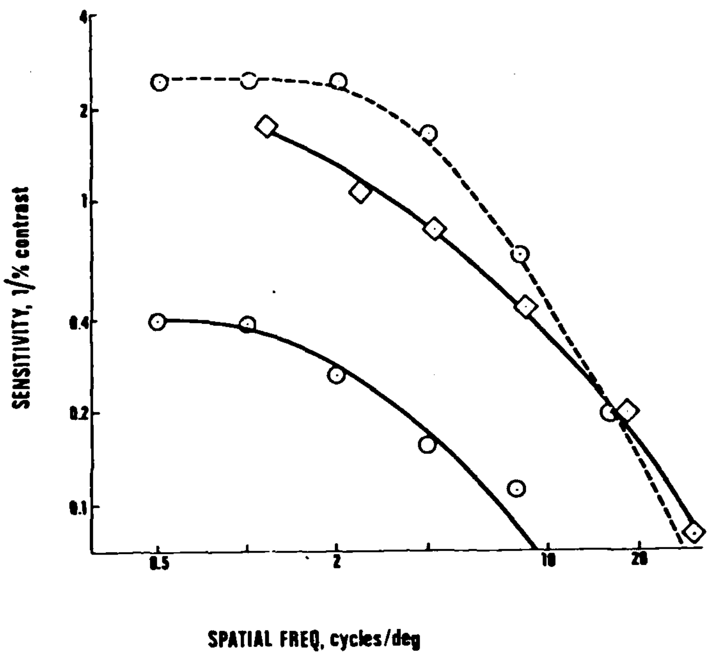
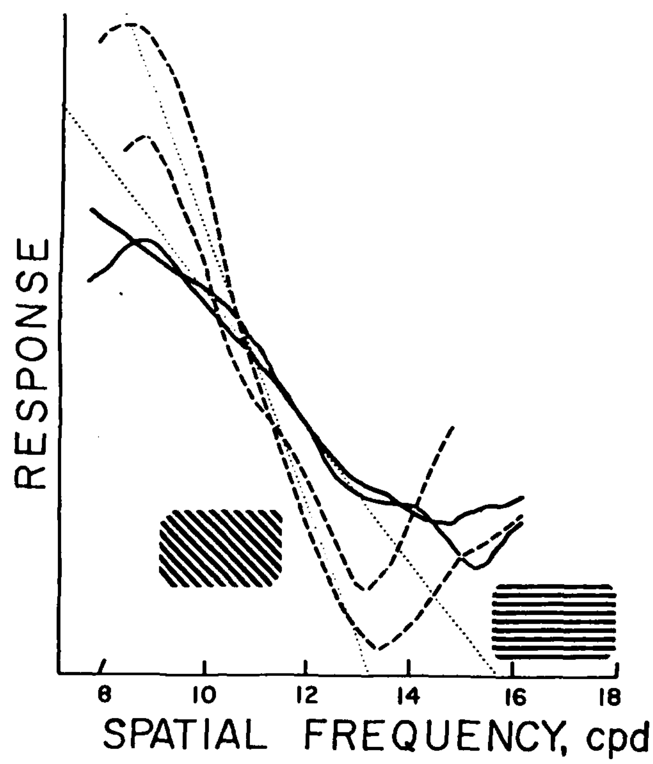


Fig. 6



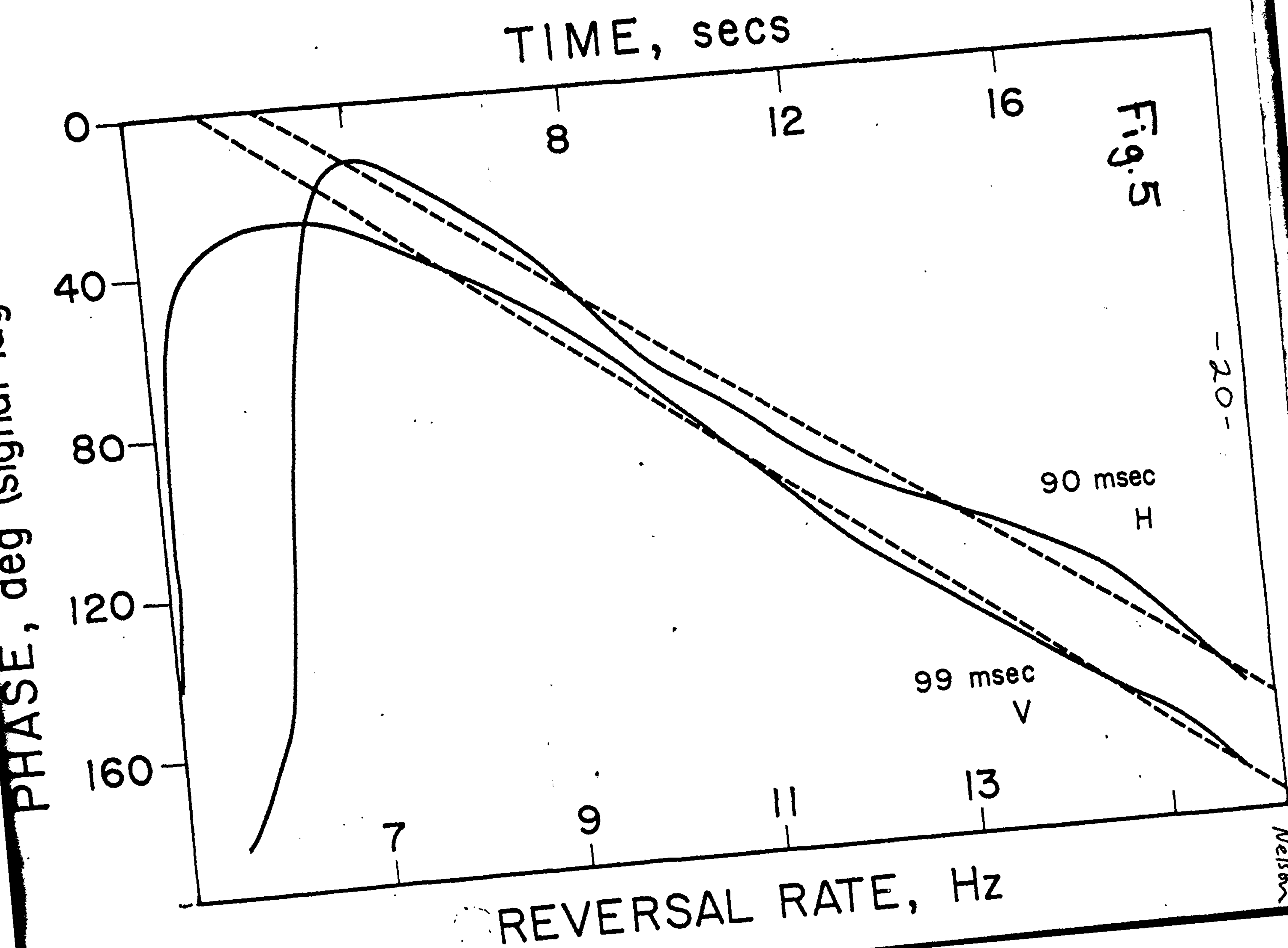
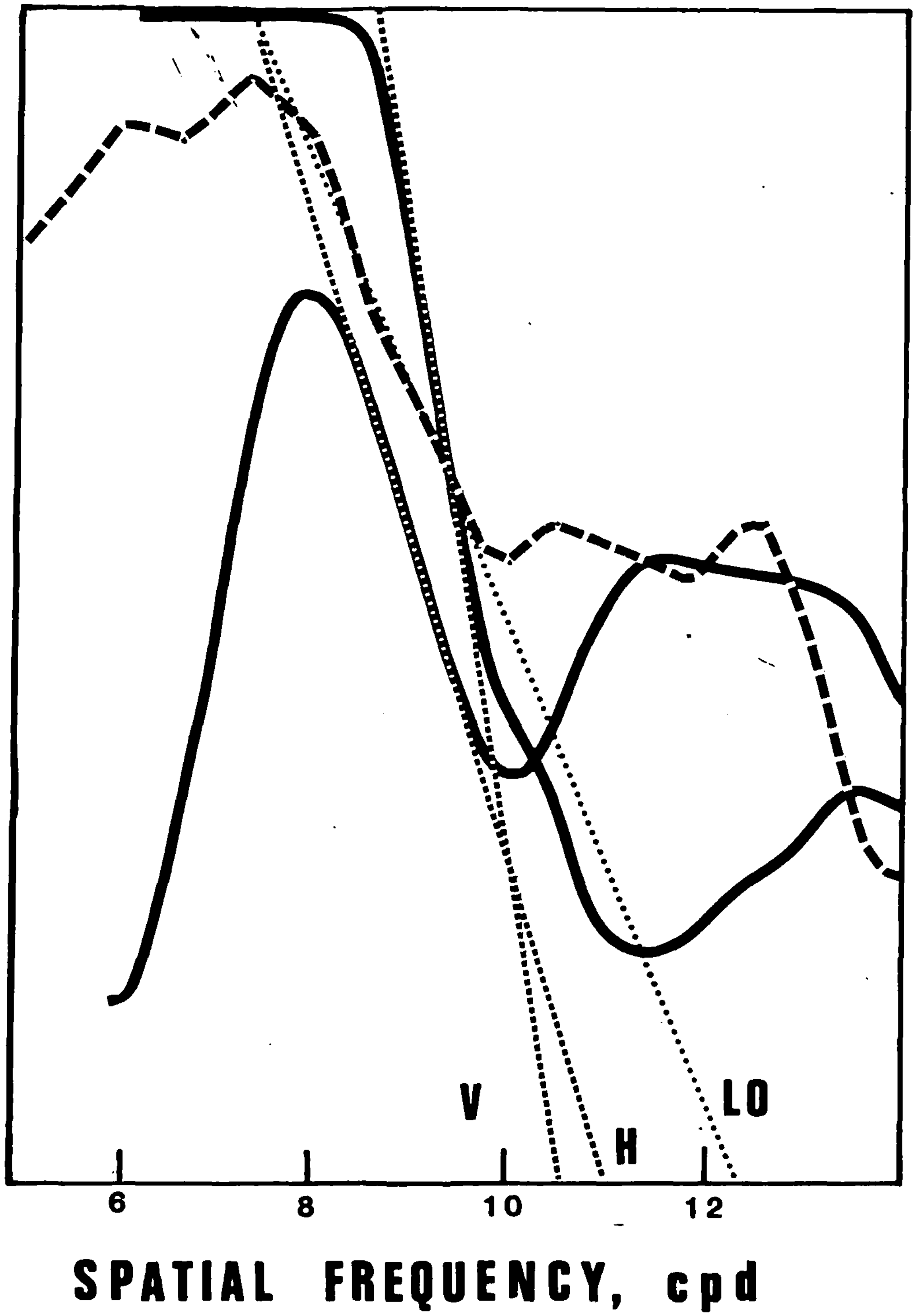
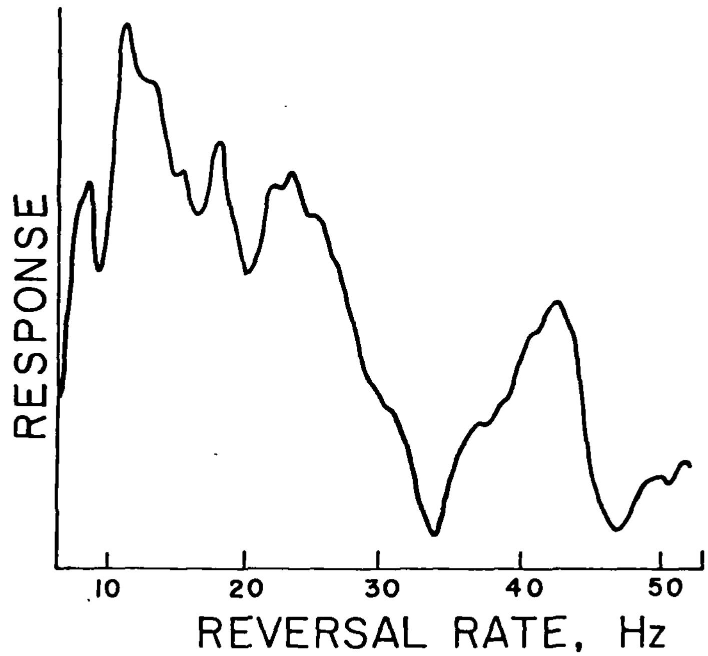
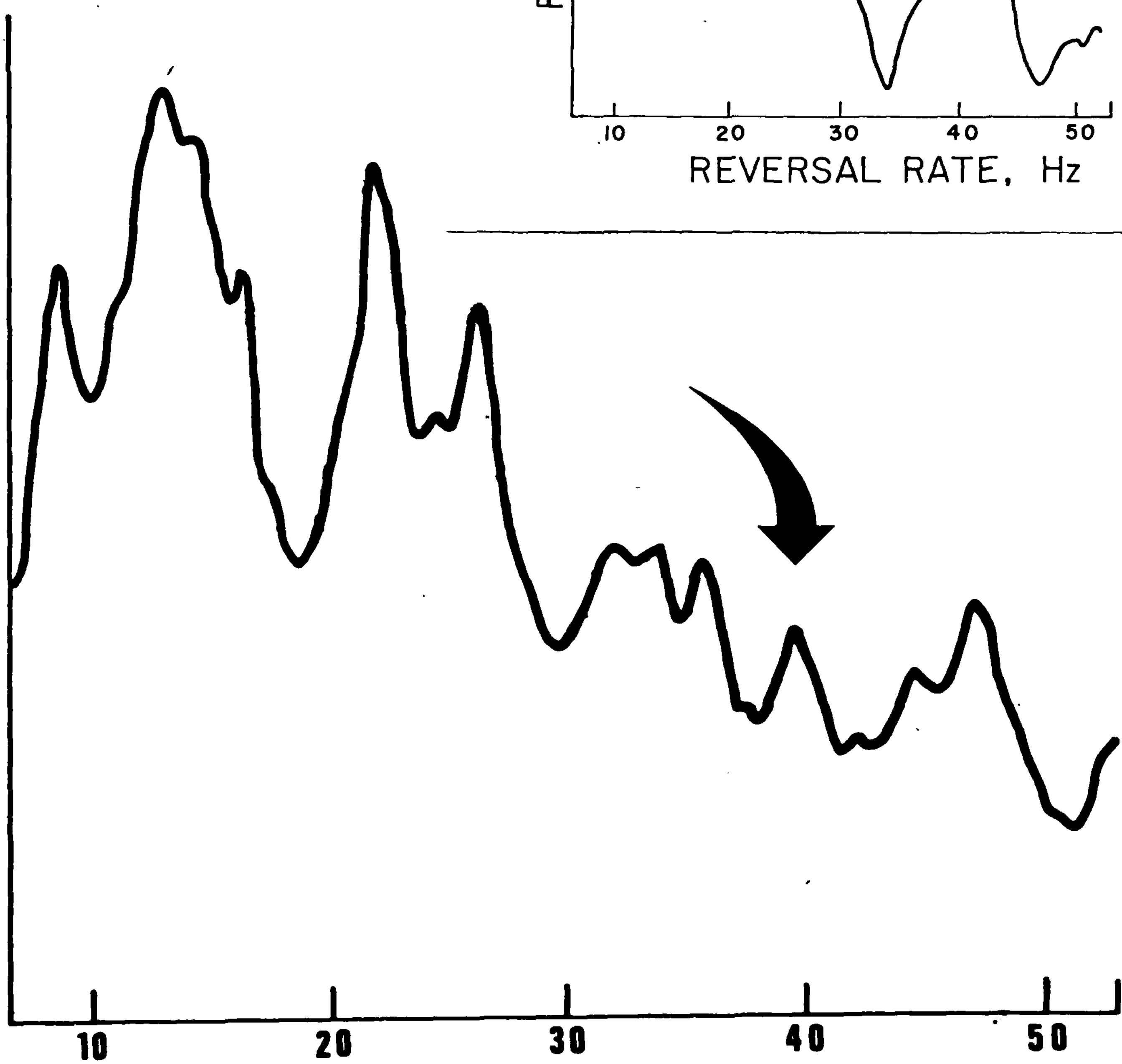

TIME, secs
8
12
16
0
40
80
120
160
PHASE, deg (signal lag re ref)
90 msec
H
99 msec
V
7
9
11
13
REVERSAL RATE, Hz
Nelson

Fig.5


V
H
LO
6
8
10
12
SPATIAL FREQUENCY, cpd

Figs. 8, 9


RESPONSE
10
20
30
40
50
REVERSAL RATE, Hz


10
20
30
40
50
REVERSAL RATE, Hz

DAT
FILM